J. Cons. int. Explor. Mer, 36(3): 277–281. Février 1976.

In praise of Petersen

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C. G. J. Petersen distinguished between his "growth" theory and the then current "propagation" theory when accounting for the reduction in catches (and sizes) of flatfish in the Kattegat during the late eighties and early nineties of the last century. There is a current distinction between growth overfishing and recruitment overfishing, to which Petersen's earlier contribution is highly relevant. Therefore it was worth recalling how he came to this conclusion and what was the climate of opinion on these problems at that time. His methods are worth exposition in themselves and serve a strongly didactic purpose at the present time.

Introduction

In a study of the history of the international fisheries commissions (Cushing, 1972), a distinction was drawn between growth and recruitment overfishing. In the former, recruitment is not affected, but weight of catch is lost because fish are caught before they have had a chance to grow. When recruitment overfishing occurs, the magnitude of the incoming year-classes declines as stock in numbers is reduced. Demersal fish grow in weight by as much as an order of magnitude during their adult lives, and their stocks are vulnerable to growth overfishing as a consequence, but because of their high fecundity (and perhaps high capacity for stabilization) tend to resist recruitment overfishing. Pelagic fish do not grow very much during their adult lives, so their stocks cannot suffer from growth overfishing, but because they are not very fecund (with possibly a low capacity for stabilization) they succumb to recruitment overfishing. On re-reading Petersen's (1894) paper, I noticed that almost the same distinction was made, when discussing possible remedies for the decline in catch and in mean size of flatfish, particularly of the plaice of the Kattegat. This paper summarizes the reasons that led Petersen to make the distinction eighty years ago.

During the last two decades of the nineteenth century both the catches and the average sizes of fish were declining. In Britain, the commissions of 1866, 1879 and 1884 examined the state of the fishing industry by taking evidence from fishermen and scientists. A wasteful destruction of immature fish was though to be the cause, despite the fact that McIntosh's evidence collected at sea (given to the 1884 commission) did not appear to support the thesis. In his inaugural address to the International Fisheries Commission (1884) T. H. Huxley said that the seas were inexhaustible.

Huxley's argument was as follows: cod live in a layer 120–180 feet thick off the Lofoten Islands and they live one yard apart, so there are $1{\cdot}2 \times 10^8$ beneath one square mile. The area is much more than one square mile and the total catch is $0{\cdot}3 \times 10^8$. A similar argument was applied to quantities of herring eaten by cod there and Huxley wrote: "Facts of this kind seem to me to justify the belief that the take of all the cod and herring fisheries put together does not amount to 5% of the total number of the fish. But the mortality from other sources is enormous ... I believe then that the cod fishery, the herring fishery, the pilchard fishery, the mackerel fishery and probably all the great sea fisheries are inexhaustible ... that is to say that nothing we do seriously affects the numbers of the fish." In other words, recruitment overfishing was inconceivable. In the same volume, Lankester (1884, p. 416) wrote something quite different: "When the fisherman removes a large proportion of soles from a given area, and so reduces the number of young soles born in the same season in that area, he does not simultaneously destroy the natural enemies of the young sole: consequently very nearly the same number of young soles are destroyed, by such natural enemies as were so destroyed before man interfered, although very many less young soles are produced." Thus the opinion of the two leading zoologists in Britain in 1884 was that if fishing were to affect the stocks, it would reduce recruitment, but that in fact catch was a very low fraction of stock, or the seas were inexhaustible.

A decade later, the discussion was formed between four scientists. First, Fulton (1890b) and Holt (1891) showed that immature fish were in fact caught in large numbers and they considered this harmful to the reproductive capacity of the stock. Secondly, Petersen drew the distinction between the "growth theory" and the "propagation theory", saying that the important effect was the fishing on the older and bigger fish and that reproduction was probably not affected. Thirdly, Garstang (1900) showed decisively that a decline in stock density had occurred that was associated with a rise in fishing effort. In the early arguments in the "Overfishing Committee" in the International Council for the Exploration of the Sea (until about 1905), Petersen and Garstang discussed the "small plaice" problem: large quantities of very small plaice were then being caught off the coasts of Holland and Germany. Their analysis was that of a problem in growth overfishing, but they were defeated by the variability of the material (see an account in Cushing, 1972).

The contribution of Fulton and Holt

Fulton (1890b) measured 13000 whitefish in trawl hauls and examined their degree of ripeness and estimated the sizes below which they were immature. He studied the distribution of immature fish of different species inshore and offshore, by length, by depth and by distance offshore. The proportion of immature fish was high and the implication was that fish should have been allowed to reproduce at least once. He wrote "A consensus of opinion that the supply of most of the valuable flatfish ... has fallen ... it has also been shown that the young are destroyed in large numbers." Fish were tagged (Fulton, 1892) with brass numbered discs tied to the tail with black silk; of 3000 to 4000 fish tagged (Fulton, 1893) about 5% were recovered (8·2% of plaice) in about the position of tagging, which showed that this stock remained in the fishery. In 1891 it was shown that fish returned to the sea would live and in 1894 that they would escape through larger meshes in the cod-end into a cover. However, these pioneer experiments did not lead towards a control of the stock by mesh regulation in the sense that we consider it today. Fulton (1890a) wrote that a controlling mesh size would not be very practicable and the protection of immatures in declining fisheries "has not been effective... it has been found necessary to supplement restriction by artificial cultivation". A number of papers were written on fecundity and spawning and in 1893 an artificial hatchery was established in Dunbar (Fulton, 1893).

Holt (1893) reported Fulton's work on the length at maturation and showed that of catches in the North Sea of plaice, the majority (2212280 out of 2664200) were below the "biological size limit" (i.e. the length at which they become mature). He wrote "Everyone ... admits that a fish should have a chance of spawning before it is killed." However, he noticed two effects. The first was the loss of the older, bigger fish; in the early period of exploitation old fishermen who had worked on the Dogger during the days of the early fishery referred to very large plaice of very poor quality, with brown instead of red spots, which were called "elephants' lugs". The second effect noticed was the concentration of trawlers on the very small plaice in shallow waters off the Dutch and German coasts: "If the market could once be cleared of the immense quantities of small plaice which flood it during the summer months, an improvement in price ... would be one of the first results." A solution to this problem was a reasonable size limit for flatfish and alternatives were to close the eastern North Sea in summer or to send the smacks to Iceland. Thus to Fulton's biological argument, an economic one was added. It was an important one for, as reported by Heincke (1913) during this period, as much as six times as many fish were discarded as retained on the "small plaice grounds" off the coasts of Holland and Germany. The phrase "small plaice" had at this time three distinct meanings: (a) immature (Fulton); (b) discarded for market reasons (Holt) by the fishermen; and (c) too small to have gained enough weight for an optimal catch (Petersen).

Later, Holt (1895) examined "the small plaice problem" in the catches; "in a whole year's trawling, on all North Sea grounds, 57%, or more than half, of the fish had never had a chance of reproducing their species and so contributing to the upkeep of the supply". The ideal condition would be that "the grounds should hold the greatest possible head of fish."

Thus the British interpretation of events was that the decline in stock density and loss of larger fish would lead to a form of recruitment overfishing. The cure was to impose a "biological size limit" (so that no immature fish were caught) and possibly to encourage artificial propagation. It was no accident that all the beautiful work in Britain on the rearing of larval fish during the last decade of the nineteenth century was a direct response to the interpretation of decline as being due to recruitment overfishing.

Petersen's contribution

Before his study of the plaice was attempted Petersen made some comments on the nature of populations in the sea. He set down his view on races before Heincke published his meristic measurements of herring in 1898 and before Mendel's work was rediscovered by Bateson in 1902. In Petersen's view a stock "propagates generation after generation with the *peculiar stamp of the race*" and he went on to say that "we have to prove that peculiarities (for example, the number of fin rays) have not been produced by the natural conditions for each single individual in the first generation". He was a geneticist before the science existed and before Heincke had exploited meristic measurements. He observed that one "form" of plaice lived in the Kattegat and another in the Belt Seas and the Baltic, whereas the eggs and larvae must be closely intermingled. There were alternative explanations: 1, the eggs and fry of one form die when carried into the territory of the other; 2, the eggs and fry of one form develop into those of the other under the natural conditions and he believed that the second supposition was necessary. He was right in that differences in growth and in the numbers of fin rays are considered now to be environmentally determined, at least on a limited scale; such views could only be modified in the light of strict genetic evidence, such as is now being collected on the North Atlantic cod. However, the first alternative survived in Petersen's mind because he believed that the very obvious loss of eggs and larvae were in the main due to physical causes.

The major contribution was the establishment of the ages of the younger length modes of plaice and other flatfish. Three gears were used: prawn catchers (of bobinet) used whilst wading on the shore; sandeel seines (of coarse linen); and plaice seines with small meshes; both seines could be used as shore seines or as anchor seines. Between 1891 and 1893, 238 hauls were made on the Danish coasts. Three size groups of fish were found, 1–1·5″ (Danish inches), 2·0–2·5″ and 6·5–10·0″, and they lived at distinct depths, as shown by a particular series of hauls made at 2, 3, 4, 5 and 6 fm. The three groups were named 0-, I- and II-groups, fish in their first, second and third summers; it had been shown by Hensen's (1884) egg survey and by catches of spawning fish that the plaice were winter spawners. Larger fish were grouped into a III-group, which today would include older age groups; Petersen limited his analysis to these groups and indeed called the plaice a "triennial" species. He showed that towards the end of the year the length distributions of the II- and III-group tended to amalgamate.

In order to check growth with age, Petersen invented a tag; two numbered buttons of bone were fastened behind the dorsal fin with silver wire. He noted that as much as one-third might be returned within a fishing season, but the important result for him was that from 1000 II-group fish of about 7–10″ released in spring in the Limfjord, 57 were recovered in the following October and November at lengths of 13–14″. Thus the length differences were expressed in time as growth and the length modes could be properly allocated to the right ages.

Although the adult population was called the III-group, Petersen observed that the mean length of this group had declined in the Kattegat. He cited the existence of much larger plaice elsewhere, including Iceland, but the most important evidence was the disappearance from the Kattegat and western Baltic of large, lean and unpalatable plaice sometimes called "Hanser" or "Praesteflyndere" (priest flounders). They were presumably like the "jellied plaice" found off Newfoundland (Templeman and Andrews, 1956) and "elephants' lugs" on the Dogger and however interesting such observations are as possible evidence of senescence, Petersen merely used the observations as indicating the greatest length of plaice. The "jellied" plaice are particularly interesting because they were discovered at the start of the exploitation of the fishery for American plaice. The water content of the muscle was high and the protein content was low. The degree of jellification was greatest in the oldest fish (about 60% in the length group 68–77 cm; of probably 20–25 years of age (Pitt, 1973)). In this context, the observation of Greer Walker (1970) that the number and diameter of myofibrils in white muscle of cod decreases in old age is of considerable interest.

Because the plaice was considered a stationary fish (that is, there was no evidence of migration out of the Kattegat as might be expected in fish such as herring or mackerel) the simplest explanation was that the fishery had taken the larger fish. He noticed that during the twenty years before his observations, seines had replaced gill nets and in his words, "an older troublesome way of fishing (had given way to) a later and intensive one". He suggested that *fishing power* (sic) may have increased by a factor of twenty or thirty and he cited some statistics to support the assertion and, much more to his point, the mesh sizes had dropped from 7″ to 4½″ between 1880 and 1893. He established the profit by sizes of plaice on the market at Copenhagen and wrote: "If we fish the plaice while they are small, we do not get so great a profit ... as we ought to have."

Petersen then stated the main principle, that a fleet should take "exactly so much as the stock could reproduce by new growth". He means the growth of individuals and not the growth in numbers of a population, for he showed that the natural mortality should be low; the fish were not obviously diseased and were not found in the guts of the only potential predators, cod and marine mammals. Of fish that reached 10″, a large proportion should have reached 14″ if they were protected, and would produce "a much greater quantity of meat every year".

Petersen then wrote that this was his "growth theory in contradistinction to other propagation theory". Holt (1893) and Fulton (1890b) had already suggested that a "biological limit" be established to take care of spawners. In Petersen's words, the object would be "to enable the fish to spawn in greater multitudes than formerly, in order to augment their numbers, it being supposed that the fishery has prevented them from doing so". Fulton had suggested that the numbers of individuals in the stock would be safeguarded if fish were not caught until they had spawned once. However, Petersen had been impressed by the immense quantity of eggs as shown by Hensen's estimates and "nor have I ever been able to believe in any want of small plaice . . . it is not the beginning, but in the middle and the end of the life of the plaice that we must look for the injury; for it is here that man interferes as a most troublesome factor!". He was fully aware of the dangers of reducing recruitment by fishing. "I will not deny that it is possible to fish up a species to such a degree that there are not left individuals enough for the breeding of them, but I believe that we are far from that point with the plaice." So far as can be seen, this statement may well still be true for the plaice.

Discussion

After eighty years, it is still unlikely that the plaice stocks in the North Sea or the Kattegat have suffered from recruitment overfishing. Further, because of the nature of the stock and recruitment curve, additions of larvae to the sea, as suggested by Fulton and Holt, are not likely to be effective unless the stock suffers heavily from recruitment overfishing; then the best remedy is to reduce fishing quickly. The annual recruitment to the southern North Sea plaice population is of the order of 10^8, or $3 \cdot 10^9$ on the beaches. If the density-dependent processes are by then complete, $3 \cdot 10^9$ late 0-group fish are needed to double recruitment, which is a formidable quantity with present technology.

The important point is that Petersen in two years grasped enough of the essential biology of the plaice to establish his growth theory. The subsequent formulations of the problem by Graham (1935) and by Beverton and Holt (1957) were built on the foundations laid by Petersen. Indeed, their awareness of the possibilities of recruitment overfishing was precisely the same as his – possible, but improbable. Although today we are much more aware of the problem of stock and recruitment, the step made by Petersen was of fundamental importance. Fishes must maximize their biomass during their adult lives and for the same reason fishermen must maximize their catches in weight. The order of argument has been to estimate the maximum catch with constant recruitment – the solution to the problem of growth overfishing – and only then to approach the problem of varying recruitment with parent stock. It is a parsimonious procedure.

If we look back to the concepts of Huxley and Lankester on one side (the theoreticians of the day) and to those of Fulton and Holt (the field ecologists), there is nothing in their arguments that should not convince us. However, the great step made by Petersen eighty years ago was to grasp the resilient nature of the fish population: that the numbers of young fish on the beaches were adequate to support greater catches in weight if the nature of growth in fishes were understood. Although he was fortunate in the particular gears used by the fishermen at that time, the biology of the animals was very sharply and clearly understood. When intellect is lucky, the combination is most formidable. If there is a lesson for us today, it is that we should steer between theoretician and fishery ecologist and try to understand how the populations sustain themselves.

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